International Journal of Odonatology, 2020
Vol. 23, No. 1, 5–8, https://doi.org/10.1080/13887890.2019.1682372

Charlie Ellington (1952-2019) – a career in animal flight mechanics

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Charles Porter Ellington was born on December 31st 1952 in the State of Maryland, grew up there and in the State of Georgia, and gained his first degree at Duke University, North Carolina, all in the USA. Under the leadership of Steven Vogel and Stephen Wainwright, Duke at that time was the hub of biomechanics in the USA, and several of Charlie's near contemporaries went on to establish influential laboratories on other US campuses. He took a different route, coming to Cambridge in 1972 on a prestigious Churchill Scholarship to work for a PhD under the supervision of Torkel Weis-Fogh, a brilliant Dane who was then the world leader in insect flight research.

Weis-Fogh had recently broken new ground in aerodynamics. Using high-speed cinematography of the tiny wasp *Encarsia formosa* in free flight, he had described the first non-steady state mechanism for generating high lift by flapping wings. Charlie's remit was to develop and extend this approach to other insect groups and to work towards a greater understanding of the aerodynamics of hovering flight. Disaster struck soon after, when Weis-Fogh took his own life. Charlie's supervision was taken over by Ken Machin, a radio-astronomer turned zoologist whose outstanding experimental flair lay behind much important research in Cambridge at that time.

The result was a PhD thesis that must rank among the most remarkable in the history of the degree, and spectacularly demonstrated what the disciplinary breadth of the American undergraduate system could achieve in an outstanding student. Building his own digitiser and using a computer the size of a wardrobe Charlie developed the first methodology and software for kinematic analysis of unimpeded flapping flight, and applied them to his own high-speed films of a range of hovering insects. He identified five new unsteady mechanisms for lift generation, and, crucially, was the first person to develop a vortex theory for flapping flight. He developed and extended the use of morphometric parameters in calculating aerodynamic and inertial forces and power requirements of flight. The work was published virtually intact in 1984 in a seminal series of six papers in Philosophical Transactions of the Royal Society B, and established the platform on which virtually all subsequent research on insect flight mechanics has been built.

Now on the staff at Cambridge, Charlie replaced Weis-Fogh as the recognised world leader in insect flight mechanics. An excellent theoretician as well as a first-rate experimentalist, he began a programme of research and publications with a succession of postgraduates and post-doctoral assistants, primarily addressing the nature and relative importance of unsteady mechanisms in

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insect flight, the energetics of flight at various speeds, and the efficiency of flight muscle. A brief, entertaining collaboration with myself led to the first rigorous paper on the aerodynamics of the origin of insect flight.

In this consistently excellent body of work one can recognise two highlights. In the late 1980s Charlie and Ken Machin greatly improved the sensitivity of a commercially available oxygen analyser and linked it to a small closed-circuit wind tunnel. Bumblebees were tricked by optical stimuli to fly unimpeded but geostationary in the tunnel at a range of airspeeds in front of a high-speed cine camera, with their oxygen consumption simultaneously recorded. This beautiful experiment led to a paper in *Nature* with Machin and physiologist Tim Casey exploring the variation in oxygen uptake with flight speed, and to two papers with graduate student Robert Dudley investigating in detail how bumblebee kinematics, aerodynamics and power input and output change with speed – the first time this had been achieved for any insect.

The second high spot came in the mid 1990s, with the ‘Flapper’. This was a delightful robotic hawkmoth, computer-controlled to emulate the wing kinematics of the tobacco hornworm moth which were being studied in the lab by Alexander ‘Sandy’ Willmott. Frequency was adjusted to the appropriate Reynolds Number, and smoke was emitted at appropriate points on the wing so that the airflow could be studied. Willmott’s results were at the same time sent to Hao Liu in Japan, as the basis for a computational flow model. This led to the discovery, confirmed by all three methods, of a persistent vortex above the wings’ leading edge that spiralled outwards along the span, generating high unsteady lift throughout each half-stroke. Perhaps the most important discovery in animal flight studies since the 1984 papers, the leading edge vortex has since been found in many other flying animals, and has been a major focus of attention internationally for two decades. The Flapper had its public debut at the Royal Society Soirées in 1991: see the photograph. Charlie was elected to Fellowship of the Royal Society in 1998, and in 1999 to a chair in the Cambridge Zoology Department, where he had also been recognised as an outstanding teacher, his annual course in biological mathematics being particularly highly rated.

While all his research is indirectly relevant to dragonflies, Charlie’s only direct work on Odonata was in the 1990s, through a PhD project by James Wakeling comparing the kinematics, aerodynamics and energetics of *Sympetrum sanguineum* and *Calopteryx splendens*, the first, and so far the only investigation of its kind into members of the order.

Charlie had been seriously diabetic since childhood, and in the 1990s his health began to deteriorate. He continued to supervise students, and a number of leading scientists from Europe, the US and Japan visited his laboratory to work, collaborate and publish with him. He took early retirement in 2010 to live quietly with his wife, Stephanie, in a village near Newmarket. In 2018 his health underwent rapid deterioration, and he was seriously ill in hospital for several months. Partly recovered, he spent six more months at home, but died peacefully on July 30th 2019.

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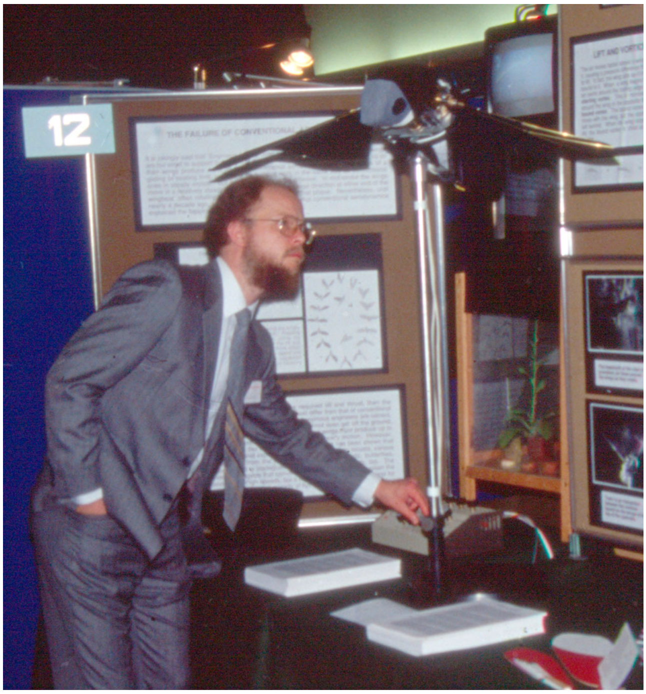

Charlie Ellington with the ‘Flapper’ at the Royal Society Soirees in 1991. The Soirees are full-dress affairs; it is just visible that the Flapper is in evening dress, ready for the evening event.

References

Dudley, R. & Ellington, C.P. (1990a). Mechanics of forward flight in bumblebees. I. Kinematics and morphology. *Journal of experimental Biology*, *148*, 19–52.

Dudley, R. & Ellington, C.P. (1990b). Mechanics of forward flight in bumblebees. II. Quasi-steady lift and power requirements. *Journal of experimental Biology*, *148*, 53–88.

Ellington, C.P. (1984a). The aerodynamics of hovering insect flight. I. The quasi-steady analysis. *Philosophical Transactions of the Royal Society of London (B)*, *305*, 1–15.

Ellington, C.P. (1984b). The aerodynamics of hovering insect flight. II. Morphological parameters. *Philosophical Transactions of the Royal Society of London (B)*, *305*, 17–40.

Ellington, C.P. (1984c). The aerodynamics of hovering insect flight. III. Kinematics. *Philosophical Transactions of the Royal Society of London (B)*, *305*, 41–78.

Ellington, C.P. (1984d). The aerodynamics of hovering insect flight. IV. Aerodynamic mechanisms. *Philosophical Transactions of the Royal Society of London (B)*, *305*, 79–113.

Ellington, C.P. (1984e). The aerodynamics of hovering insect flight. V. A vortex theory. *Philosophical Transactions of the Royal Society of London (B)*, *305*, 115–144.

Ellington, C.P. (1984f). The aerodynamics of hovering insect flight. VI. Lift and power requirements. *Philosophical Transactions of the Royal Society of London (B)*, *305*, 145–181.

Ellington, C.P. (1985). Power and efficiency of insect flight muscle. *Journal of experimental Biology*, *115*, 293–305.

Ellington, C.P. (1991). Aerodynamics and the origin of insect flight. *Advances in Insect Physiology*, *23*, 171–210.

Ellington, C.P., Machin, K.E. & Casey, T.M. (1990). Oxygen consumption of bumblebees in forward flight. *Nature*, *347*, 472–473.

Ellington, C.P., van den Berg, C. Willmott, A.P. & Thomas, A.L.R. (1996). Leading edge vortices in animal flight. *Nature*, *384*, 472–483.

Liu, H., Ellington, C.P., Kawachi, K., Van den Berg, C. & Willmott, A. (1998). A computational fluid dynamic study of hawkmoth hovering. *Journal of experimental Biology*, *201*, 461–477.

Wakeling, J.M. & Ellington, C.P. (1997a). Dragonfly flight. 1. Gliding flight and steady state aerodynamics. *Journal of experimental Biology*, *200*, 543–556.

Wakeling, J.M. & Ellington, C.P. (1997b). Dragonfly flight. 2. Velocities, accelerations and kinematics of flapping flight. *Journal of experimental Biology*, *200*, 557–582.

Wakeling, J.M. & Ellington, C.P. (1997c). Dragonfly flight. 3. Lift and power requirements. *Journal of experimental Biology*, *200*, 583–600.

Willmott, A.P., Ellington, C.P & Thomas, A.L.R. (1997). Flow visualisation and unsteady aerodynamics in the flight of the hawkmoth *Manduca sexta. Philosophical Transactions of the Royal Society of London (B)*, *352*, 303–316.

Wootton, R.J. & Ellington, C.R.P. (1991). Biomechanics and the origin of insect flight. In *Biomechanics in Evolution* (ed. J.M.V. Rayner & R.J. Wootton). Pp. 99–112. Cambridge, Cambridge University Press.